Bull. Mus. Comp. Zool., Harvard Univ., 127(9): 451-478, Oct. 1962.

No. 9 — *The Anoles of the Eastern Caribbean (Sauria, Iguanidae) Parts IV-VI*

TABLE OF CONTENTS

IV. The Anoles of the Northern Leewards, Anguilla to Montserrat: New Data and a New Species.

By Ernest E. Williams

INTRODUCTION

Initially, as I have stated in the preface to the first part of this series (Williams, 1959), I felt that the Museum of Comparative Zoology collections provided an adequate survey of the anoles of the Lesser Antilles. We had relatively large series of most of the forms recognized, and representatives of all. Many of the specimens were types or syntypes of Garman's or Barbour's names. There were indeed doubts about the application of certain older names, but this was felt to be a purely nomenclatorial problem that could wait upon an opportunity to solve it. There appeared to be very plausible grounds for the belief that a very satisfactory beginning in the revision of the *Anolis* of this limited region could be made by a study of the collections of this one museum — a museum that had a tradition of interest in the region.

As it has worked out, this belief has proved quite wrong. Basic to this error was an assumption that has proved fallacious: the assumption that these small islands could harbor but one or, at a maximum, two species of *Anolis* per island. Where there were as many as two, Barbour had already provided a neat categorization that seemed also an explanation: there were a rupicolous and an arboricolous series.

Underwood (1959) has commented on the taxonomic philosophy of Garman and Barbour which reasoned from the reality of distinct forms on some islands to the existence of endemics on every island. But neither he nor I at the beginning questioned the assumption of extreme faunal restriction and minimal faunal differentiation.

I have now had the opportunity to study many specimens not available to Underwood in the summer of 1957. I have examined the material at the American Museum of Natural History as well as material from the Chicago Natural History Museum, the University of Michigan Museum of Zoology, and also United States National Museum specimens seen by Underwood briefly or not at all. I have received for determination the anoles collected by Walter Auffenberg and J. Wayne King in the Leeward Islands in the summer of 1958. Specimens from Antigua, Montserrat, and Dominica collected in 1958 have been donated to the MCZ by James D. Lazell, Jr. (Over 500 anoles were collected on Dominica by Lazell in 1959. He here publishes separately on the anoles of this island.) Previously I had received live specimens sent up by Underwood in the course of his collections. Kodachromes of some of these are at hand, as well as kodachromes prepared by J. Lazell, Jr., and notes on color in life by Wayne King, Underwood, Lazell, Proctor and others have been available. Live and preserved anoles collected by G. R. Proctor have been repeatedly donated to the MCZ via Underwood. In 1961 National Science Foundation Grant NSF-G16066 provided funds for a Caribbean tour which permitted me to see in the field *Anolis trinitatis*, *A. roquet aeneus*, *A. roquet roquet*, *A. bimaculatus leachii* and *A. wattsi*.

This quantity of previously unreported material supplements Underwood's (1959) presentation, restoring certain names abandoned by him, adding new forms, and hinting at complications still to be recorded. It may be true that the Lesser Antilles provides us with the simplest segment of the genus *Anolis* but this, if it be true, promises tasks in other areas formidable to the point of fantasy. What is here provided is a continuing progress report.

The *bimaculatus* group on the northern islands

Basically the situation seems clear and neat for the members of the *bimaculatus* group in the northern islands from Anguilla to Montserrat. Each bank of the Leewards supports a single

form of the *Anolis bimaculatus* group, and each form is unmistakable on color alone. "Color" is here understood to be color in life; preservation in strong formalin reduces the varied shades present in life to an undistinguished and unpleasant brown and destroys all but the most prominent patterns. Even alcohol loses much of the colors of life and may retain one only — and that not the most frequent — of a repertoire of patterns possible to each individual of a species. I here summarize the presently available evidence for all representatives of the *bimaculatus* group south to Montserrat. I include at the end of each discussion some remarks on the few distinctive scale characters of the several forms, since these were not stressed by Underwood in his presentation: these scale characters are few indeed and modal rather than absolute. I have employed for each form the trinomials used by Underwood, although I have lingering doubts that e.g. *gingivinus* is really conspecific with *bimaculatus*. I find in the case of these island forms, for which the test of sympatry or parapatry is unavailable, the arguments for "splitting" as little compelling or persuasive as those for "lumping." The conventional standard of the degree of difference of valid sympatric forms does not apply in *Anolis*. Forms that in morphology and color are quite distinct may intergrade; forms that are just distinguishable may be full species. I regret that Linnean nomenclature compels decisions which the evidence cannot warrant.

Anolis bimaculatus gingivinus

Notes are available on colors in life for *gingivinus* both in Anguilla and St. Martin. For Anguilla there are notes by both Auffenberg and King on their own collection and also by Underwood for three specimens sent him by G. R. Proctor. I collate their remarks below; I have ventured to combine their slightly varying remarks the more confidently since anoles differ not only from individual to individual but from moment to moment.

Ground color of dorsum dark brown to gray, the gray streaked and spotted with brownish gray or dark brown or with obscure diamonds dorsally. A white or gray stripe from neck above to hind leg. Tail banded with light and dark, sometimes with bronzy sheen at base. Venter light brown or gray. Orbital scales dark brown. Iris black. Dewlap deep yellow orange to umber.

King's description is the only one at hand for St. Martin. He found the *gingivinus* there very similar to Anguilla specimens except that "one was a pale green; none of the Anguilla anoles ever assumed a green color."

This interesting difference in color repertoire may possibly be correlated with a behavioral difference that King noted. For Anguilla, he states: "I noticed a lack of anoles in the trees and bushes — the anoles that I see are always on the rocks or scurrying through the brush. . . . I collected anoles on the hillside north of the salt pond. Almost every large rock not surrounded by weeds had an anole sunning itself on it. The rocks seem to provide the anole with a good view of the surrounding area for they all darted behind the rock no matter what side they were approached from."

In St. Martin, on the other hand, King very specifically mentions catching anoles "from the rocks and trunks of trees." Queried as to this point, he is quite emphatic (letter of March 1, 1959): "Both Dr. Auffenberg and myself feel that the anoles on St. Martin are more arboreal than those on Anguilla. On St. Martin I collected them in trees, bushes and on rocks. To my knowledge I didn't collect a single anole on a tree or bush while on Anguilla. Although I rather doubt it myself, this may be a reflection of the numbers of available trees — Anguilla is very, very scrubby."

The middorsal scales are strongly enlarged in all *gingivinus*, almost as prominent as in members of the *wattsi* group, but in contrast to the conditions in the latter the ventrals in *gingivinus* are quite smooth.

Anolis bimaculatus sabanus

No fresh or live material of this form has come to hand. In this animal, however, the preserved specimens probably give a fairer image of color in life than is true in any other case. The very bold well-spaced spotting (dark brown on light, almost regular), the absence of any flank stripe, and the white belly color are well shown in the alcohol preserved types in the MCZ. The extreme boldness of the pattern is absolutely distinctive, not approached by any other *Anolis*.

There is no enlargement of the middorsal scales in *sabanus;* the ventrals are smooth.

Anolis bimaculatus bimaculatus

I collate below Auffenberg's and King's notes on the color in life of Nevis *bimaculatus*.

Ground color of dorsum yellow green. Flank stripe green or yellow, rarely white. Tail gray or green (blue green) with at

least indications of darker crossbands. Venter yellow white. Head pastel blue or blue green, upper labials and neck yellow. Orbital skin green or light yellowish green. Iris black. A black spot usually present just over front limbs. Dewlap light yellow.

Miss Cochran's (1934) description of a St. Eustatius animal from color notes by Dr. Paul Bartsch is more elaborate:

"The top of the head in front of the eyes is peacock-blue, the larger scales with a pinkish flush that becomes intensified behind the eyes and on the temporal region. The pineal eye is gray brown. The side of the head anterior to the eyes is peacock blue. The area about the eyes is intense brilliant green. The top of the nape is blue with a pinkish flush. The main dorsal part of the body is yellowish green from the nape to the tail. This color extends from the base of the tail over the fore and hind legs, but these have a yellowish pink superimposed, which gradually fades into yellow-green on the belly. On the throat, and from there to the fore leg, are irregularly distributed spots of orange, the posterior portion being uniform in color. The inside of the legs corresponds in color with the belly. The posterior half of the upper side and the outside of the hind legs are marked with obscure spots of blue. An inch behind the base of the tail the same peacock blue seen on the forehead reappears, slowly grading from the general dorsal color. The last two inches of the tail are pale brown. Here spots and splashes of dark brown, blue, and various shades of rose are irregularly scattered about. The median under part of the tail is a little paler than the ground color of the rest, and free from spots on the outer half, the posterior inch of the coarse scaled portion being brown."

Miss Cochran quotes Dr. Bartsch as remarking of Nevis caught *bimaculatus*: "— the blue-green one here is not so beautiful as on St. Eustatius."

King's comments on St. Kitts animals indicate local difference here also: "The yellow shoulder stripe in these lizards is very intense and we saw none in which the stripe was white as in some of the Nevis specimens. They are very large here, some reaching a foot in length and are bluer on the head and tail than the Nevis ones." Underwood has commented that St. Kitts animals are chalky green rather than blue green and that creamy markings are more extensive on the head.

Miss Cochran has commented that the Nevis specimens available to her lacked the shoulder spot characteristic of the animals from St. Eustatius and that the St. Kitts specimens were intermediate — the spot slightly apparent. The reduction or absence

of the shoulder spot in Nevis specimens is very well borne out by the preserved specimens in the MCZ as is the small size of the shoulder spot in St. Kitts specimens. On live Nevis specimens Auffenberg comments, "the large males have a black spot on the body just over the front limbs — however this is quite variable." King states: "There are black spots dorsally and laterally on the back and hind legs and tail. These spots are present only in large males, absent in small ones. Just dorsal to the white shoulder stripe there is a large black spot about the size of the ear opening — one on each side."

In regard to spotting, other than the shoulder spots, preservation produces results very difficult to interpret. In some series the specimens are rather consistently flecked with discrete small spots all over the dorsal surface of head, body and tail. In other series from the same island spotting is inconspicuous or absent. Some formalin preserved specimens show transverse markings and mottlings or even very erratic discolorations. Important as color is in the taxonomy of *Anolis*, it must be used with discretion.

The middorsal scales are somewhat enlarged and sometimes swollen in *bimaculatus* but grade quite gradually into the flank scales. The ventrals are always smooth.

Anolis bimaculatus leachii

Auffenberg provides a color description for *leachii* from Antigua: Ground color light bright green. Tail greenish at base fading into greyish brown over most of its length. Head greyish to brownish speckled or mottled with dark brown or black, "this pattern extending over the shoulders and entire dorsum of some specimens." Dewlap yellowish orange.

Preserved specimens show considerable variability in dorsal speckling and vermiculations. As Underwood has indicated, the spotting tends to coalesce to vermiculations anteriorly but remains discrete posteriorly. Half grown animals appear to show at least occasionally bolder spotting than large adults, but in all cases with much individual variation. (Formalin preservation emphasizes the spotting more than does alcohol preservation; in life also the same individual will show bolder or less bold spotting in different phases.) Sometimes the spots coalesce more or less longitudinally to give the impression of broken lines. In all cases, however, the lower flanks in front of the thighs show no vermiculations and minimal spotting.

Large males have the middorsal scales very distinctly swollen and noticeably but not greatly larger than the adjoining scales. The ventrals are usually smooth.

Anolis bimaculatus nubilus

I have had the opportunity to examine freshly-preserved specimens of this form collected for the United States National Museum. There is, however, no color description from life.

From the preserved animals it is evident that the characters noted by Underwood — almost no trace of flank stripe and light speckling most pronounced in the hind limbs — hold good in the new material. This form seems quite peculiar and distinct in that, at least in preservative, speckling appears to be almost confined to the hind quarters. This is in strong contrast with the Antiguan animal which both in life and in preservation is vermiculate anteriorly — i.e., the speckles are there confluent — and in which even the speckling is reduced posteriorly. The Redonda form is equally different from the Desirade animal in which in all preserved specimens vermiculation is present both anteriorly and posteriorly. The fresh Redonda specimens differ also from the Desirade specimens in the absence of any bright pigment on the orbital scales. In Redonda animals of a general tan body color, these scales are blue gray as preserved.

On the evidence of the new material there is no doubt that the Redonda form is as distinct as is any of the other *bimaculatus* color races, but the lack of knowledge of color in life makes the comparisons incomplete.

The middorsal scales are distinctly larger than the lower flank scales but grade quite gradually into those alongside them. The ventrals are smooth.

Anolis bimaculatus lividus

Underwood has very well described this form. I quote his description with the color variations (or differences in interpretation?) noted by Auffenberg and King in brackets.

"The predominant color is bright yellow green [bright green, pea green] grading to blue [blue green, light blue; "the intensity of the color makes it appear almost fluorescent"] on tail. There is russet [bright orange, red orange] around the eye and a variable extension of russet [brownish, yellowish brown, rust brown] onto the head and forequarters. Oblique rows of pale spots were sometimes present on the sides. The belly is yellow [light yellow to white]. The flank stripe is never strongly defined and is very variable in its extent. These lizards can turn a warm brown [uniform brown, olive]. The fan is light ochre

[light yellow to orange].'' The pale spots on the sides show in a few of the specimens preserved by King. Whether this is a constant character of some specimens or a phase that any individual might sometimes assume, I do not know.

The middorsal scales tend to be enlarged and swollen. The ventrals are weakly keeled.

The *wattsi* series

Specimens of a small anole with strongly keeled ventrals, the keels in line and with two middorsal rows enlarged, are known from Anguilla, St. Martin, St. Eustatius, Nevis, Barbuda and Antigua, unknown on Saba, St. Barts, Redonda, Montserrat, or any isle to the south except for St. Lucia, where this form has only recently been discovered in the port city of Castries (Underwood, 1959, p. 217).

Two nominal species have been described in this series: *A. wattsi* Boulenger 1894 (type locality: Antigua), *A. forresti* Barbour 1923 (type locality: Barbuda). Underwood (1959), without discussing the matter, has placed *forresti* in the synonymy of *wattsi*. In this action he appears to be fully justified; the characters cited by Barbour (1923) in the type description do not hold, and no other characters to distinguish *forresti* and *wattsi* have been found.

Synonymy of *wattsi* and *forresti* is not surprising. The two type localities — Barbuda and Antigua — are islands of one bank with similar ecologies. Underwood was unable (as I am also) to distinguish between the *bimaculatus* representatives on these two islands.

It was somewhat more surprising that the animals from Anguilla, St. Martin, St. Eustatius, St. Kitts and Nevis appeared to be the same as those from Barbuda and Antigua. This was at variance with the situation in the *bimaculatus* group in which each bank had its own well marked form. However, Underwood had seen both the Antiguan and St. Kitts populations in life and had found only trivial color differences. It seemed clear, therefore, when Underwood wrote that *wattsi* was a single form which had undergone hardly any differentiation on the several islands and banks that it inhabited. Underwood, indeed, used *wattsi* as his illustration of ''the process of colonization of a group of islands.'' He said, ''we have the absence from the southeast (i.e., the southern Lesser Antilles) and the slight measure of differentiation between the islands as evidence of relatively recent arrival from the west.''

This conclusion seemed at the time of its writing as plausible to me as to Underwood. It was, therefore, a very real surprise when Auffenberg and King discovered in Barbuda a second species of the *wattsi* group.

Derby Cave, the area in which the new species was first found, was an extremely peculiar habitat — a sink hole in the limestone highlands to the east of Codrington, Barbuda. Wayne King has vividly described the sink hole and its environs:

"The area surrounding the sink hole is scrubby — seldom reaching over twenty feet — woods. Cactus, both "organ pipe" types and low rambling "Opuntia" types are plentiful. Most of the trees and bushes are thorny. There are numerous outcrops of limestone in the area, and very little soil except in

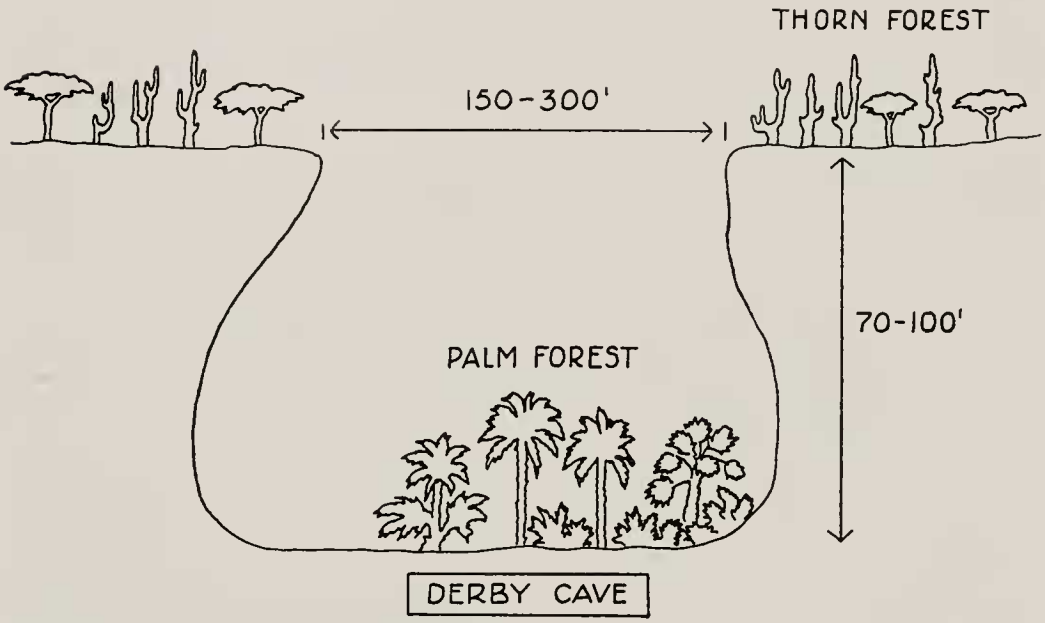

FIGURE 1. Sketch (after field sketch by Walter Auffenberg) of the ecological situation at Derby Cave, Barbuda.

pockets between the outcrops. The sink measures roughly 100 yards across and 80 feet deep. The south side is a sloping pile of rock and rubble; this is the only side which can be used to enter the sink. The other sides, in particular the north side, are sheer drops to the bottom. The north side is overhanging. The bottom of the sink is a loamy clay, dark brown to red in color. There is a dense stand of trees in the bottom. The dominant tree is a palm very similar in appearance to the cabbage palm of Florida, except it is very slender. The trunk of the palm is seldom over six inches in diameter, but trees may be 40 feet tall.

There are many small palms — young ones. Another tree which is abundant is a Ficus — growing mainly on the rock slope on the south side of the sink. The top of the sink is about 150 feet elevation.''

It was on the trunk of the palms that the new species was taken. It was immediately recognized as distinctive on color alone. I compare in parallel columns the color of Barbuda and Antigua *wattsi* and the new species.

wattsi	*new species*
Dorsum greenish brown to brown but base of tail and most of its length translucent yellow or light orange.	Dorsum uniform dark gray or brownish gray or brown to drab olive green.
Top and sides of head including orbital scales translucent yellow or light orange but temples blue gray.	Head without yellow, orbital scales green. No blue gray on temples.
Hind limbs without red markings.	Thighs with red or rusty bands which on the posterior aspect are free of dark overlay and thus appear as brilliant orange spots.
Belly bright yellow.	Belly not yellow.
Dewlap yellowish orange.	Dewlap light green.

The new species was later seen or taken at other localities on Barbuda and Antigua:

1. Dark Cave, 6-7 mi. SE Codrington, Barbuda: anoles seen in shallow sink in which the cave occurs.
2. Bryant Cave, 6-7 mi. SE Codrington, Barbuda: a large sink similar to Derby Cave with a pool of ground water at bottom.
3. Gaynor's Mill, 1 mi. W, 1½ mi. S. Willikies Village, St. Philip's Parish, Antigua: a thick growth of trees with a high canopy growing on the broad flood plain of the river that empties into Nonsuch Bay.

The specimens from these localities differed from those from Derby Cave where the form was first found only in having *white* rather than *red* spots on the posterior edge of the thighs.

The two additional Barbuda localities closely resemble Derby Cave; the Antigua locality is similar in its dampness, high trees and shade.

The color (especially dewlap color) and habit differences reported by Auffenberg and King are in themselves adequate to diagnose the new species. However, the color differences have wholly disappeared in the preserved specimens before me. I have, therefore, strenuously endeavored to find scale differences. I have not been able to find them. Nevertheless, I regard the species status of the new form as unquestionable. Maintenance of sharp color difference, including dewlap color difference, in several small, isolated colonies is for me clear evidence that gene flow does not occur.

As the newly discovered member of a species pair, the new species may receive a Latin name meaning the other one of two and is thus called:

Anolis alter sp. nov.

Type: UF[1] 12457; Derby Cave.

Paratypes: UF 12458-1,2,3,4; MCZ 64345-8, same data.

Referred specimens: UF 12459, Bryant Cave; UF 12460, Gaynor's Mill.

Diagnosis. Closest to *A. wattsi* Boulenger but differing in the absence of yellow on snout and tail, in having a green rather than an orange-yellow dewlap. Differing as well in habitat, being confined to moist shaded areas instead of open dry conditions.

Description. Head scales smooth or at most weakly keeled. Five to seven scales across head at level of second canthal. No frontal depression.

Supraorbital semicircles broadly in contact, partially separated from the supraocular disks by one row of granules on each side. Supraocular disks consisting of *ca.* 5 enlarged scales, separated from the series of overlapping supraciliary scales by 3 rows of keeled subgranular scales. Canthus sharp, canthal scales 5, the first largest, decreasing regularly anteriorly. Loreal rows 4. Temporal scales very small, smallest in center, bounded above by a moderately distinct double line of supratemporal scales. Interparietal slightly smaller than ear, separated from the supraorbital semicircles by two scales, flanked laterally and posteriorly by scales markedly larger than the body scales.

Anterior frontal moderate but less than half the size of anterior supraorbital, separated from the first canthal scale by one scale a little larger than itself.

[1] Florida State Museum, University of Florida, Gainesville.

Four suboculars in contact with supralabials, the subocular series not continued behind the eye, continued forward by two large scales and meeting canthal ridge with no smaller scales intervening. Five to six supralabials to center of eye.

Mentals a little longer than wide, three small granules inserted between their posterior tips. Only one sublabial on each side in contact with the infralabials. Central throat scales small, cycloid, keeled.

Two middorsal rows enlarged, keeled, less than twice adjoining scales which grade gradually into keeled flank scales. Ventrals much larger, keeled, imbricate. Enlarged postanal scales present.

Dewlap scales as large or a little larger than ventrals, keeled, closely packed.

Scales of upper and lower limbs unicarinate, of digits multicarinate. *Ca.* 17 lamellae under phalanges 2 and 3 of fourth toe.

Tail compressed with a strongly enlarged middorsal row of enlarged scales, three per verticil. Lateral scales keeled, large, in 4-5 rows. Ventrally 3 pairs of scales per verticil, somewhat enlarged.

Size: Type, 42 mm snout-vent length.

Comment. Squamation in the *wattsi* group is not by any means uniform. There is variation in the size and crowding of the middorsal enlarged scales, in the degree of keeling, and, to a less degree, in the size of the ventrals. There is also evident variation in the size of the flank scales.

None of these characters, however, appears to be fully useful taxonomically. The size and crowding of the middorsal scales is a sexually dimorphic character: the adult males and females of typical *wattsi* may be accurately sexed by examination of the middorsal scales alone. At one time it seemed possible that *alter* might be distinguished by the less swollen, smaller middorsal scales of the males, more similar to those of females, than in *wattsi*. However, there is a size factor in this sexual difference and when the smaller males of *wattsi* are compared with the available males of *alter* the difference, while probably still real, becomes so subtle as to approach invisibility. The largest male of *alter* is only 42 mm; males of *wattsi* approach 50 mm. There may be a real difference in maximum size here, but the material does not exist to demonstrate the point.

Some of the Nevis specimens of *wattsi* collected by King are near maximum for the species and yet appear to have markedly

smaller middorsals and small flank scales and less keeled ventrals than Antiguan specimens of the same size. Other Nevis specimens, smaller in size (MCZ 38375-6), have significantly larger middorsals and larger flank scales and well keeled ventrals. It is possible that distinct forms are here being confused but without additional information I am compelled to regard the differences as "individual variability."

Color, thus, seems to be the only useful character; the colors in this instance are not likely to be saved even by preservation in alcohol rather than in formalin. Reds and yellows are notoriously fugitive in alcohol and are retained only for a limited period in formalin. The spots on the hinder side of the thighs so much emphasized in the descriptions of live *alter* by King and by Auffenberg are present in all members of the *wattsi* group; they are apparently merely less conspicuous in brown and yellow *wattsi* than in green and red or green and white *alter*. In preserved specimens there is no perceptible difference. A blue tinge appears on the temporal region of Antiguan and Barbudan *wattsi;* this is absent in the *wattsi* of the St. Kitts-Nevis bank. It will, even in preserved specimens, assist in the recognition of *alter* as compared with sympatric Antiguan-Barbudan *wattsi.*

We are left, therefore, with no secure means of telling all preserved *alter* from all preserved *wattsi.* For identification we need data on ecology and on color in life. These are thus true sibling species — since "sibling," here as always, means difficult to tell apart by the *conventional* methods of the taxonomist.

I would, indeed, lack the courage to describe *Anolis alter* if I had not renewed my acquaintance with live *wattsi* by a visit to Antigua in December 1961 and if Walter Auffenberg had not procured for me live *alter* from Derby Cave in March 1962. The color differences which I have listed above for these two species (p. 462) are fully confirmed. The orange so conspicuous on snout, chin, tail and dewlap in live *wattsi* is quite absent in live *alter*. The sole difference which the new collections reveal is that the red spots on the thighs cited for topotypic *alter* in the collections made in the summer of 1958 are in the March-caught specimens of 1962 dull orange. This difference may reflect seasonal changes. At all events it only slightly diminishes the clear-cut difference between the two forms, and is all the less important since *red* markings on the hinder side of the thighs are always absent in non-topotypic *alter*.